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Psammophores: Do Harvester Ants (Hymenoptera: Formicidae) Use These Pouches to Transport Seeds?

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ABSTRACT: *Pogonomyrmex* ants have a psammophore or basket of long hairs under their heads which they use for carrying loose soil. The presence of these hairs or ammochaetae improved the carrying ability of *Pogonomyrmex occidentalis* workers and queens by more than 200% for dry soil but provided no benefit for damp soil. Foragers readily used their psammophores to collect small seeds and particles of cracked wheat from artificial bait piles. Psammophores were profitably used with particles up to 0.8 mm^3 or about 1.2 mm diameter. Removal of either the mandibular or subgenal portions of the psammophore significantly reduced carrying ability but did not completely destroy its function. *Pogonomyrmex* workers clearly have the capacity to use their psammophore during foraging and its use could distinctly improve foraging efficiency; nevertheless, foragers apparently do not use this pouch under natural conditions. *P. occidentalis* foragers did not begin using the psammophore until seed densities were far above normal (>0.5 per cm^2) and full loads were only achieved at extremely high seed densities (>10 per cm^2). The main problem was that once a forager accepted a food item, no matter how small, it immediately returned directly to the nest without searching for a second item.

The name "*Pogonomyrmex*" means "bearded ant". Ants in this genus received this name because they possess a cluster of long hairs extending off the ventral surface of their heads (Fig. 1). These hairs are collectively termed a psammophore from the greek words "psammos" and "-phor" meaning "sand carrying" (Santschi, 1909). Spangler and Rettenmeyer (1966) firmly established that these hairs function as a basket or pocket for carrying loose particles of sand. Workers load their psammophores by tucking particles up into this pocket using their forelegs and the tip of their abdomen (Wheeler and Wheeler, 1963). Once the pocket is full, the mandibles are closed and the mandibular hairs fit over the pocket like the lid on a basket (Fig. 1). Similar structures have been observed in other ants living in arid regions of the world including species from such genera as *Myrmecocystus, Pheidole, Cataglyphis, Melophorus, Messor, Ocymyrmex, Monomorium* and possibly *Dorymyrmex* (Wheeler, 1907; Wheeler and Wheeler, 1973). Bernard (1948) found psammophores on about one-third of desert species he examined. Certain digger wasps which inhabit dry or sandy areas also possess a psammophore (Evans, 1966, 1981).

The purpose of this study was to investigate further the function and value of psammophores in the western harvester ant, *Pogonomyrmex occidentalis*. We were particularly interested in determining if the psammophore is used as a foraging pouch to retrieve multiple food particles. Such a behavior would be very similar to the foraging strategy of pocket mice and could substantially improve foraging efficiency by decreasing the number of trips necessary to harvest small food items. Retrieving multiple seeds could also allow relatively large ants like

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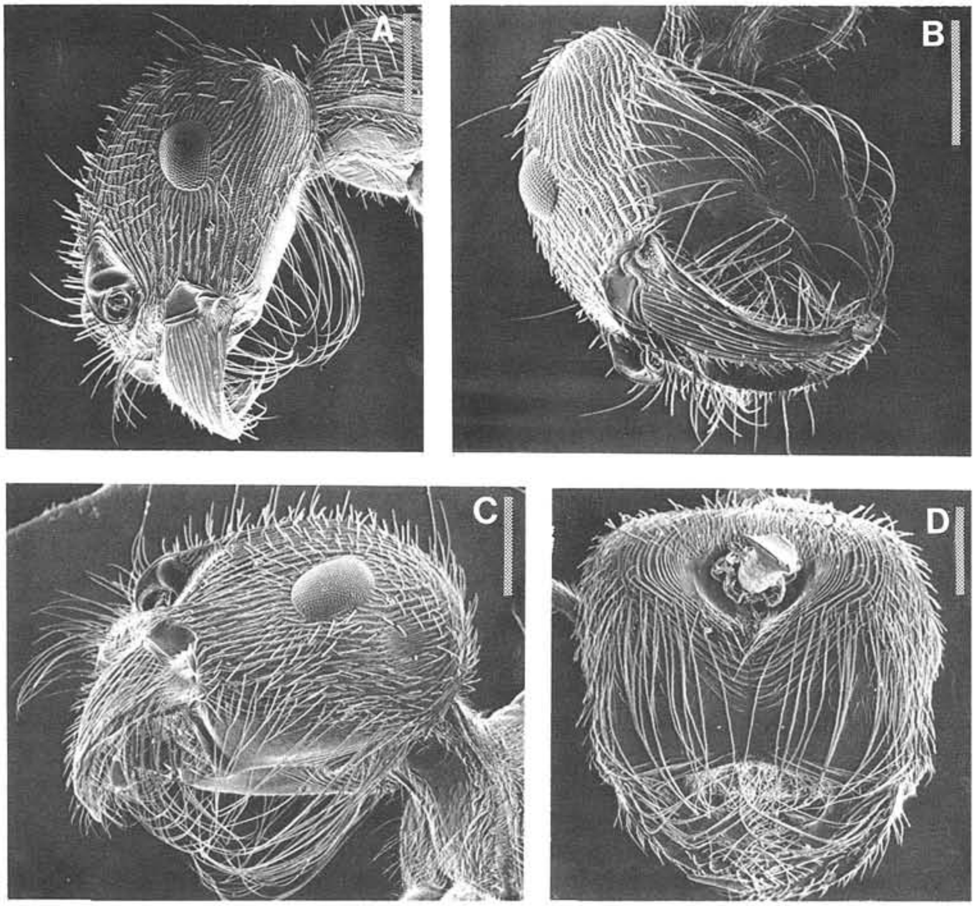

Fig. 1. A) *Pogonomyrmex occidentalis* worker, lateral view of psammophore showing pocket formed by long recurved hairs extending off ventral surface of head. B) Ventrolateral view of worker psammophore. C) Psammophore on founding queen. D) Head of queen showing ventral view of psammophore. Grey bar on each view indicates 0.5 mm.

P. occidentalis to utilize seeds that would normally be too small to justify foraging expenses.

Materials and Methods

Most of our studies were conducted at sites in Utah Valley, Utah during the summer of 1986. Field tests were centered along the eastern slope of West Mountain. Scanning electron micrographs were taken using standard techniques. Prior to electroplating, workers were immersed in a soap solution and cleaned in an ultrasonic vibrator.

SOIL EXCAVATION: The value of a psammophore in carrying soil was determined by comparing the average load carried by untreated control workers with loads carried by treated workers lacking psammophores. Psammophores were removed by immobilizing 20 experimental ants on crushed ice and carefully plucking the hairs off the mandibles and subgena using fine forceps. Twenty control ants received the same manipulations except their hairs were not removed. Ants were allowed to recover at room temperature for 3 hr before being tested. We induced soil excavation by placing control and experimental ants in separate 15 cm diameter plastic petri dishes with a 2 cm hole cut in the bottom along one edge. Sides of the dishes were coated with fluon (Wilson, 1978) so the workers could not escape. The dishes were then placed firmly on a tray of loose dry soil. Workers excavated the soil and dumped it on the floor of the dish where each load was aspirated into specially modified Pasture pipettes. We collected and weighed six samples of 20 excavation loads from both the treatment and control groups. At this point water was added to the soil until it was moist but not saturated. Six more samples of 20 loads from each group were collected, dried, and weighed. The entire process was replicated with ants from two colonies. A similar protocol was used to investigate the value of psammophores to founding queens, except the queens were allowed to excavate individually.

FORAGING: Cracked wheat particles of different sizes were used to determine the potential use of psammophores for foraging. Particles were sieved into five size categories using a stack of six U.S.A. standard sieves (Numbers 12, 16, 18, 20, 30, and 35). Particles collected on the top sieve (No. 12) or passing through the bottom one (No. 35) were discarded. The volume of an average particle collected on the remaining five sieves was: 1.48 (16), 0.69 (18), 0.48 (20), 0.17 (30), and 0.09 (35) mm^3. Volumes were calculated from average weights based on a constant of 0.76 mm^3/mg.

Particle size and number retrieved: We used three field colonies to study how particle size affects the number of items which individual foragers can carry. Piles of successively larger sizes of cracked wheat were placed about 2 m from each colony. Fifteen foragers were collected as they left each pile and the number of particles carried by each ant was counted.

Psammophore removal: The following experiment was conducted to determine how much the psammophore increases a forager's ability to carry different sizes of seeds. A laboratory colony was connected to a foraging arena with a 2.5 m runway. We collected 60 foragers and set up four treatments with 15 workers each. Psammophores in the first treatment were totally removed, only the subgenal hairs were removed in the second treatment, and only the mandibular hairs in the third. These latter two treatments allowed us to compare the relative importance of the mandibular and subgenal portions of the psammophore. The fourth group served as an experimental control. Each group was marked with a dot of silver or gold paint on either the head or thorax and returned to their colony. Five size classes of cracked wheat were offered to the colony in succession as described in the field tests. We collected returning foragers and counted the number of particles each was carrying until we had examined 16 from each treatment and size class (320 total).

Distance and load size: To determine if distance affected the number of bait particles retrieved for foragers, we alternated bait from the No. 30 sieve (0.17 mm^3) between 1.0 and 6.0 m from two field colonies, starting at 1.0 m with the first colony and 6.0 m with the second. Each distance was sampled twice at each colony, and twenty workers were inspected as they left the pile for each cycle of distance.

Density experiment: The following experiment was designed to determine how densely food items must be distributed before foragers begin using psammophores to transport multiple particles. An area of 0.25 m^2 was cleared and marked on a trunk trail about 3 m from each of four mounds. Cracked wheat (0.17 mm^3) was initially scattered across the test area at densities of 0.02 or 0.09 particles/cm^2. Fifteen returning ants were then collected, and the number of particles carried were counted. Particle density was then doubled and the returning ants examined. This procedure was repeated until we had densities of more than 10 particles/cm^2.

Results

MORPHOLOGY: The psammophore in *P. occidentalis* workers extends like a basket off the ventral portion of the head (Fig. 1A). This basket is composed of about 46 elongated hairs or ammochaetae (Wheeler, 1907). Of these 46 hairs, 32 ± 3 are located on the subgena and 7 ± 3 on each mandible. Shorter hairs are also scattered around the periphery of the psammophore. Mean spacing between the ammochaetae is approximately 0.1 mm; consequently, the psammophore can retain spherical particles as small as 0.0005 mm^3 or roughly 1 μg.

Ammochaetae on the subgena form the primary basket or pocket of the psammophore. These hairs are arranged in a single row along the lateral margins, but occur in 2–3 rows along the back margin near the occipital foramen. Ammochaetae on the subgena extend forward in a long arc which terminates above the distal margin of the head capsule (Fig. 1A). Mandibular ammochaetae extend medially to meet the subgenal hairs and form an interlocking lid when the mandibles are closed (Fig. 1C). The roof of the psammophore (ventral surface of head) is very smooth in contrast to the rest of the body; perhaps this facilitates loading and unloading of the psammophore. Most of the ammochaetae appear to be socketed and may function as sensory receptors during loading. High magnification of individual ammochaetae did not reveal any additional fine structure. Several very small hairs are located inside the psammophore pocket along the bottom of the head (Fig. 1B); these hairs may be sensory in function.

Ammochaetae on the clypeus number 11 ± 3 (Fig. 1A, B). These hairs do not actually aid in soil transport but they are probably important as a forward retainer so loose particles do not slide out between the open mandibles during loading. An empty psammophore encloses about 0.7 mm^3 in normal workers, and 0.1 mm^3 in nanitic workers (miniature workers produced by founding queens). The psammophores of queens were 40% larger than those of workers; they enclosed 1.0 mm^3 and contained more than 70 ammochaetae (Fig. 1C, D), most of the additional hairs being located along the rear margin of the subgena.

Psammophores of 15 other North American *Pogonomyrmex* species in the subgenus *Pogonomyrmex* (Cole, 1968) were also examined (i.e., *anergismus, apache, badius, barbatus, californicus, colei, comanche, desertorum, magnacanthus, maricopa, montanus, owyheei, rugosus, subdentata,* and *texanus*). Their psammophores were quite similar although the size and shape varied somewhat. Estimated volumes for workers ranged from 0.35 mm^3 in *P. magnacanthus* to 1.0 mm^3 in *P. maricopa*. The number of ammochaetae in worker psammophores ranged from 38 in *P. badius* to 60 in *P. californicus*. The psammophores of alate queens were considerably larger than those of workers (40–200% by volume). Queens of all species examined (n = 8) contained 60–80 ammochaetae on the mandibles and subgena, except *P. anergismus* which averaged only 37 and *P. colei* which averaged

38. Presumably, these two species had relatively few ammochaetae because they are social parasites and do not need to excavate their own nests during founding.

The males of most species showed no hint of a psammophore; the ventral surface their heads contained numerous fine silky hairs scattered across the surface. The two social paracites were exceptions. *P. anergismus* males had thickened ammochaetae, but no clear sign of a pocket. *P. colei* males had a rudimentary psammophore complete with thickened ammochaetae and a smooth ventral surface on the head. The function of this structure on males (if any) is not known.

Worker psammophores were best developed in the *maricopa* complex and least developed in the *badius* and *barbatus* complexes as measured by their relative volume and density of ammochaetae. Psammophores in the *maricopa* complex covered most of the underside of the head compared to only the lower two-thirds of the head in the *badius* and *barbatus* complexes. The *occidentalis* complex was intermediate. Five South American *Pogonomyrmex* species were also examined. The psammophores of two (*P. vermiculatus, P. rastratus*) were about as well developed as the *badius* or *barbatus* complexes. Three other species (*P. coarctatus, P. atratus,* and *P. micans*) had small but still clearly developed psammophores which extended only half-way between the mouth parts and occipital foramen. The smaller relative sizes of psammophores in these South American species (Gallardo, 1932; Kusnezov, 1951) may be associated with more mesic conditions in their ranges.

SOIL EXCAVATION: The presence of a psammophore greatly increased a worker's capacity to transport loose dry soil. Intact control workers carried 205% more soil than the treated workers which lacked a psammophore (Fig. 2; $t = 21.3$, d.f. $= 22$, $P < 0.0001$, log-transformation). Results for founding queens in dry soil were similar, except the difference was 260% (Fig. 2; $t = 15.4$, $P < 0.0001$, $n = 7$, log-transformation). By contrast, the presence or absence of a psammophore had no effect on the ability of workers and queens to transport moist soil (Fig. 2; $P > 0.05$). Curiously, queens carried almost three times as much soil as workers even though their psammophores were only 40% larger in volume (Fig. 2).

FORAGING: The following investigations were conducted to determine if foraging workers can use the psammophore to retrieve multiple particles of food. Older foraging workers often show considerable mandibular wear compared to younger interior workers (Porter and Jorgensen, 1981), so we initially checked the physical condition of forager psammophores and found that most were intact although a few did show minor wear.

Particle size and number retrieved: Foragers in the field readily carried back multiple particles from piles of cracked wheat. The average number of particles ($\pm$SD) carried from each size class (mean particle volume, mm^3) was: 7.5 ± 2.0 (0.09), 4.3 ± 1.7 (0.17), 2.5 ± 1.1 (0.48), 2.0 ± 0.8 (0.68), and 1.0 ± 0.0 (1.48). The corresponding load volumes were: 0.7, 0.7, 1.1, 1.1, and 2.0 mm^3. The number of particles retrieved decreased as particle size increased. Average load volumes of small bait particles were equal to the calculated volume of any empty psammophore (0.7 mm^3), but loaded psammophores apparently expand because maximum loads were about 30% larger than average loads. Workers were able to carry larger volumes of intermediate sized seed particles because one particle was usually carried in the mandibles and one in the psammophore. With the largest size of bait, only one particle could be carried at a time. Piles of cracked wheat (particle

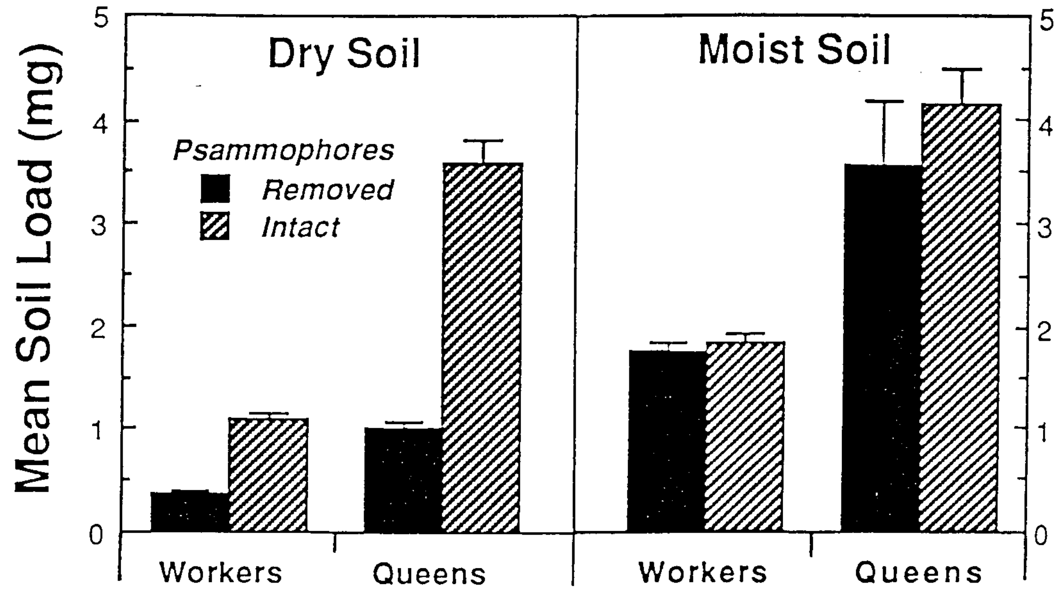

Fig. 2. Average loads (mg) of dry or moist soil carried by excavating ants in which psammophores were intact or experimentally removed. Standard errors are shown for each mean.

size: 0.17 mm^3) were also presented to colonies of *Pogonomyrmex barbatus* and *Pogonomyrmex comanche* in Austin, Texas. Both species readily retrieved multiple particles (3.9 ± 1.6 and 2.6 ± 1.3, respectively).

Psammophore removal: Treated workers with the entire psammophore removed were capable of carrying several particles in their mandibles, but control workers with intact psammophores carried significantly more of all particle sizes $\leq$0.69 mm^3 ($P < 0.001$, Fig. 3). Furthermore, the loads carried by control workers were very close to loads observed in the field colonies (see section above). The relative percent benefit (B) of using a psammophore to carry different-sized particles was calculated by: $B = (P_c - P_t)/P_t$, where P_c was the number of particles carried by control workers and P_t was the number carried by treated workers lacking a psammophore (Fig. 3). Initially, the benefit curve increased rapidly as particle size decreased (Fig. 3). With even smaller particles, the benefit curve began to approach an asymptote probably near 205%, the value observed for loose dry soil (see Fig. 2). The psammophore provided no benefit for seeds or other food items greater than about 0.8 mm^3 or 1.2 mm average diameter. This size limit agrees closely with the observations of Spangler and Rettenmeyer (1966) for large pieces of sand.

Experimental workers lacking either mandibular hairs or subgenal hairs carried intermediate numbers of particles (Fig. 4). Using Duncan's new multiple range test, both treatments were significantly lower than the control ($P < 0.01$) but significantly higher than workers with the entire psammophore removed ($P < 0.01$). Workers lacking only the mandibular hairs carried more particles than workers lacking the subgenal hairs, but this difference was not quite significant ($P > 0.05$). The benefits of the mandibular and subgenal hairs appear to be additive, since their combined increase in load capacities over workers lacking the psammophore accounted for 80–100% of the increase observed for intact control work-

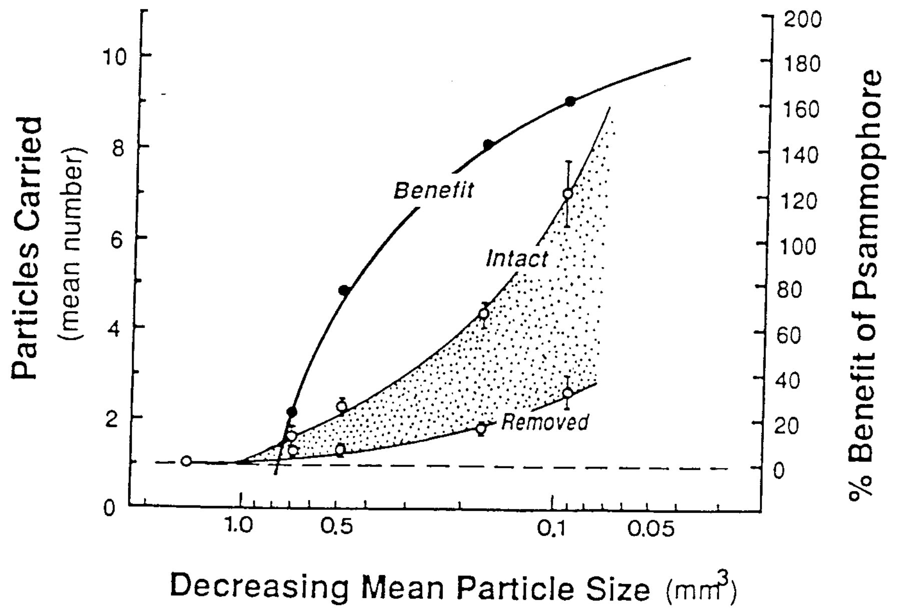

Fig. 3. Load capacity of intact control workers and treated workers in which psammophores were removed plotted against decreasing sizes of cracked wheat particles. The benefit curve plots the percent increase in load capacity attributable to the psammophore. Error bars show standard errors of the means.

ers (Fig. 4). In other words, the removal of one part of the psammophore did not destroy the function of the remainder.

Distance and load size: According to foraging theory, foragers travelling long distances to find food should be more selective because they would have more time and energy invested (Taylor, 1977; Davidson, 1978). If this is true, we reasoned that workers may be more careful to completely fill the psammophore if they travelled 6.0 m than if they traveled 1.0 m. However, the number of particles loaded into the psammophore was not affected by distance. In fact, the trend, though non-significant, was opposite that predicted; workers at 1.0 m loaded slightly more particles than did those at 6.0 m (means: 5.0 versus 4.3; $F = 8.03$, d.f. = 1,1, $P > 0.05$). The absence of a distance effect on selectivity has also been found in other seed harvesters (Rissing and Pollock, 1984).

Naturally foraged seeds: The western harvester ant can transport small particles of cracked wheat in the psammophore, but are naturally collected seeds small enough (<0.8 mm^3; Fig. 3) to be carried in this way? Approximately 89% of the seeds collected by *P. occidentalis* foragers in Wyoming (Rogers, 1974) were too big to fit in the psammophore. Most if not all seeds collected by *Pogonomyrmex desertorum* and *Pogonomyrmex rugosus* near Portal Arizona were too large to be carried (Chew and De Vita, 1980). A majority of seeds in Utah Valley were also too big for the psammophore, especially when colonies were foraging on grasses. However, colonies at several locations in the valley collected mostly small seeds ($\bar{x} = 0.30$ mg, 0.26 mm^3). This matched our results in Idaho with *Pogonomyrmex owyheei* (Jorgensen and Porter, 1982) where 70% of seeds collected were small enough ($\bar{x} = 0.11$ mg, 0.09 mm^3) to have been profitably transported in the psammophore. About 88 ± 6% (SD) of seeds removed from the granaries of three

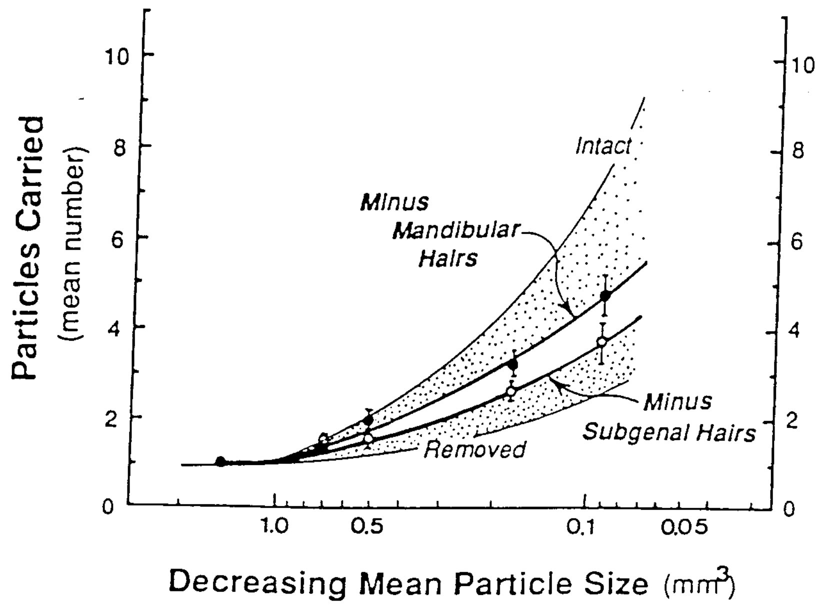

Fig. 4. Mean number of cracked wheat particles carried by workers lacking either the mandibular or subgenal portions of the psammophore. The thin lines are from Fig. 3; they show load capacity for intact control workers (upper line) and workers in which both portions were removed (lower line). Error bars are standard errors of the mean.

P. badius colonies in Tallahassee, Florida were small enough to have been carried in the psammophore (unpubl. data). Similarly, a majority of seeds harvested by *P. rugosus* at a site near Phoenix, Arizona were sufficiently small (0.08 mg; Rissing, 1988). Also, the sizes of seeds collected by *P. rugosus* and *P. desertorum* near Rodeo, New Mexico (Davidson, 1977) indicates that 20–40% were small enough to be carried in their psammophores.

Density experiment: The number of particles collected by individual foragers increased with increasing bait density but only over a range of three magnitudes (Fig. 5). Variation among replications was actually the most important single factor; it accounted for 81% of the sample variation ($F = 33.4$, d.f. = 3,4, $P < 0.001$). In a multiple regression, bait density explained an additional 5% of the variation ($t = 3.07$, d.f. = 23, $P < 0.01$). In the lab, workers without a psammophore carried an average of 1.8 ± 0.1 particles of this size bait in their mandibles (Fig. 3). Field workers with psammophores exceeded this range only at very dense bait concentrations (>0.5/cm^2) and required even denser concentrations (>10/cm^2) to achieve a full load (Fig. 5).

Use of psammophores by foragers under natural conditions: While workers readily used the psammophore to retrieve seeds from artificial bait piles, we were unable to discover foragers using their psammophores under natural foraging conditions. In Utah Valley, workers always carried one food item at a time. We observed workers carrying two small seeds on several occasions during a previous study in Idaho (Jorgensen and Porter, 1982) with the sister species, *P. owyheei*, but this was rare and did not exceed their carrying ability without a psammophore (Fig. 3). Examination of numerous *P. barbatus* foragers in Austin, Texas also failed to reveal foragers retrieving multiple particles.

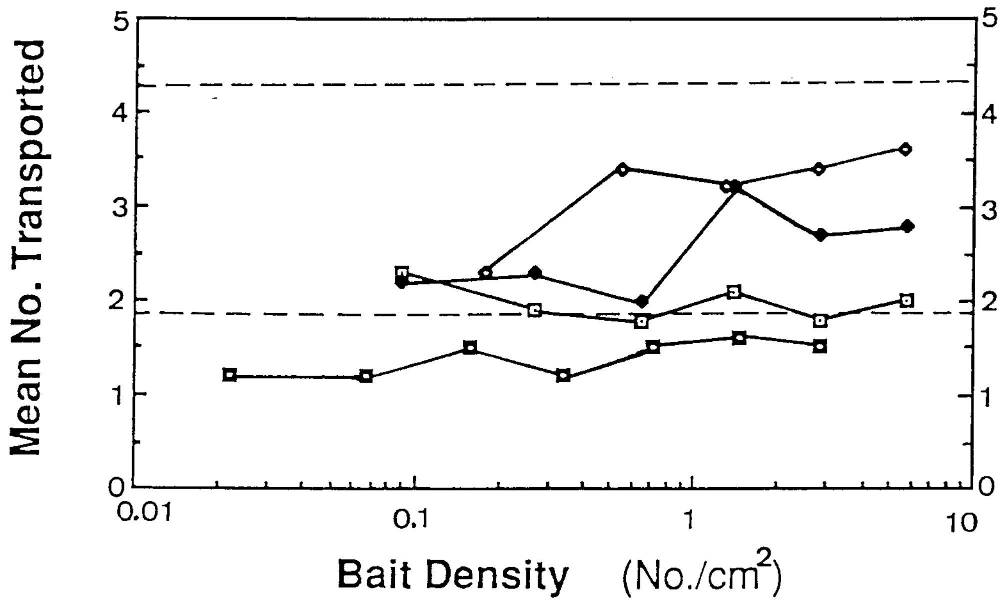

Fig. 5. Effect of bait density on the number of cracked wheat particles (mean size, 0.17 mm^3) collected by foraging workers from four colonies. Upper dashed line shows average number of particles collected at piles of bait while lower dashed line shows average at piles for workers without a psammophore (from Fig. 3).

Discussion

Psammophores are very important in transporting loose dry soil (Fig. 2; Spangler and Rettenmeyer, 1966). The presence of a psammophore increased the transport capacity of workers in our study by 205% and queens by 265% (Fig. 2). The fact that psammophores are so well developed in queens (Fig. 1C, D) is not surprising because founding queens must excavate a burrow quickly to avoid predation and environmental stresses. However, the advantage of having a psammophore essentially disappeared when workers and queens transported moist soil (Fig. 2). Ants with and without psammophores carried almost the same amount of moist soil; which helps explain why psammophores are much less common with ants living in mesic environments (Wheeler, 1907). Interestingly, the two *Pogonomyrmex* queens which were social parasites, had poorly developed psammophores, probably because they do not need to excavate.

Foragers of the western harvester ant have both the capacity and opportunity to use the psammophore during foraging. Foragers presented with piles of cracked wheat or small seeds readily loaded as many as 12 particles into their psammophores. Similar results were also observed with *P. barbatus* and *P. comanche.* The ability to carry multiple food particles was clearly due to the psammophore because its removal reduced carrying ability by 40–60% (Fig. 3). Furthermore, naturally collected food items are frequently small enough (<0.8 mm^3; Fig. 3) to be profitably transported in the psammophore (Rogers, 1974; Davidson, 1977; Jorgensen and Porter, 1982; Rissing, 1988). In spite of this capability, we were unable to discover workers using their psammophore as a foraging pouch in the field. Many other studies of *Pogonomyrmex* foraging have been conducted (e.g., Hölldobler, 1976; Rogers, 1974; Davidson, 1978; Whitford et al., 1976; MacKay, 1981), but none have reported foragers returning with multiple food items in their psammophores. Apparently, this behavior does not occur or it is very uncommon.

Two proximal factors primarily account for why psammophores were not used in foraging. The first factor is seed density. Foragers did not begin profitably using their psammophores until seed densities exceeded 0.5/cm^2 and full loads were not achieved until densities exceeded 10/cm^2 (Fig. 5). Workers only used the psammophore at seed densities far exceeding those normally found in nature. The second and most important factor was behavioral. At no time did we see a forager accept a small food item and then continue searching. Once a forager accepted a food item, no matter how small, it immediately returned directly to the nest. A second item was occasionally added only if the forager ran over it on the return trip.

If foragers do not use the psammophore for foraging, why do they use it without hesitation whenever they encounter a pile of seeds? The answer may be that workers commonly use psammophores to transport small seeds stored within their nests or even between nests when a colony emigrates (see Carlson and Gentry, 1973).

What are the reasons psammophores are not commonly used in foraging? This is a much more difficult problem because data on search times indicates that use of psammophores could substantially improve foraging efficiency. We previously found that an average foraging trip *P. owyheei* required 4 min of searching and 7 min of transit to and from the mound for a total trip time of 11 min (Jorgensen and Porter, 1982). If these ants had searched for an additional 4 min; presumably they could have discovered a second food item and returned in 15 min with twice the reward, a 45% improvements in foraging efficiency. Collecting third or fourth items would have improved efficiency by 75 and 90%, respectively. In short, use of psammophores could improve foraging efficiency by reducing transit costs to and from the nest.

However, the benefits of using a psammophore are greatly diminished when search times are much longer than transit times. Rogers (1974) reported an average trip time of 23 min over a distance of 5 m which translates into 5 min for transit and 18 min for searching assuming a transit rate of 2.2 m/min (see Jorgensen and Porter, 1982). Searching for and retrieving two, three or four food items would have improved foraging efficiency by 12, 17 and 19%, respectively. While these values are much lower, they still represent distinct improvements in efficiency.

When is it best to search for and retrieve one item per trip like most harvester ants and when is it best to collect several items per trip like a pocket mouse? The foraging strategy of collecting multiple items must be balanced against a number of impediments: 1) Low seed densities would reduce benefits by increasing search times as discussed above. 2) Many seeds are too big to be profitably carried in a psammophore; consequently, use of a psammophore would only be beneficial in certain areas and seasons when very small seeds were abundant. 3) Extending the duration of a foraging trip to collect an extra item or two may not be feasible at higher temperatures (e.g., 40–60°C; Rogers, 1974; Whitford and Ettershank, 1975). Foragers might be able to tolerate 10 min at these temperatures, but not 15 or 30 min. 4) Another problem is that extending the foraging trip would increase the lag time between discovery of a good site and recruitment of additional workers; however, a few minutes of delay would normally be offset by faster retrieval rates. 5) Extended foraging trips would also increase the chances of predation (in which case, food items already collected would be lost). However, collecting several items per trip could actually reduce predation costs by reducing the time outside the nest per food item. This would be especially true if most predation occurred during transit on trunk trails.

The above mentioned factors may diminish the value of using a psammophore to collect multiple food items; nevertheless, they do not explain why foragers should not collect multiple seeds when small seeds already compose a substantial fraction of their diet. 1) Perhaps, foragers simply do not possess the manual dexterity to manipulate another seed into the psammophore without losing items already collected. While this was occasionally true, most workers appeared quite adept at loading their psammophores, at least with the first several particles. 2) Similarly, *P. occidentalis* may not have the behavioral sophistication to use a psammophore effectively. Effective use of a psammophore would require workers to balance benefits against search times, success rates, seed sizes, predation and environmental stresses. Nevertheless, the sophistication is not unreasonable because workers already make many of these choices when foraging for single food items (Whitford and Bryant, 1979; Taylor, 1977; Davidson, 1978). 3) Harvester ant colonies have a large supply of reserve workers (Porter and Jorgensen, 1981); it could be that recruiting additional workers to dense patches of small seeds is more effective in the long run than developing the behavioral sophistication or manual dexterity necessary for retrieving multiple food items. The bottom line may be that *P. occidentalis* foragers do not utilize their psammophores simply because they have never developed the ability. In other words, this ability may represent an adaptive peak that has never been achieved.

Other *Pogonomyrmex* species apparently do not use psammophores for foraging either—judging from personal observations and dozens of publications dealing with *Pogonomyrmex* foraging. Nevertheless, most investigators have not specifically looked for its use, and most of the 60 *Pogonomyrmex* species which occur in North and South America (Cole, 1968; Kusnezov, 1951) have not been carefully studied. It is hoped that future investigators will check for this behavior specifically.

In conclusion, western harvester ants clearly have the capability to use a psammophore during foraging, and use of this pouch could substantially improve the foraging efficiency of individual workers. Nevertheless, foragers of this species apparently do not use this capability; in spite of the fact that its acquisition would require a seemingly minor change in behavior—foragers would simply need to accept a food item and continue searching rather than immediately returning to the nest.

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